

Nonocclusal Dental Microwear Analysis of 300,000-Year-Old *Homo heidelbergensis* Teeth From Sima de los Huesos (Sierra de Atapuerca, Spain)

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KEY WORDS buccal; enamel; striation; diet; Pleistocene; human

ABSTRACT Casts of nonocclusal enamel surfaces of 190 teeth from the Middle Pleistocene site of Sima de los Huesos have been micrographed by scanning electron microscopy. Microscopic analyses of striation density and length by orientation show distinct patterns of intrapopulation variability. Significant differences in the number and length of the striations by orientation are found between maxillary and mandibular teeth. This probably reflects differences in the mechanical forces involved in the process of chewing food. Significant differences are present between isolated and in situ teeth that could be caused by postdepositional processes differentially affecting the isolated teeth. In addition, a distinct and very unusual striation pattern is observed in a sample of teeth that can be explained only by a strong nondietary, most probably postmortem abrasion of the enamel surfaces. These teeth have a very high density of scratches, shorter in length than those found on other teeth, that are not indicative of dietary habits. No known depositional process may account for the presence of such postmortem wear since heavy transportation of materials within the clayish sediments has been discarded for the site. Despite this, a characteristic dietary striation pattern can be observed in most of the teeth analyzed. Most likely the diet of the *Homo heidelbergensis* hominids from Sima de los Huesos was highly abrasive, probably with a large dependence on hard, poorly processed plant foods, such as roots, stems, and seeds. A highly significant sex-related difference in the striation pattern can also be observed in the teeth analyzed, suggesting a differential consistency in the foods eaten by females and males. *Am J Phys Anthropol* 108:433–457, 1999. © 1999 Wiley-Liss, Inc.

The presence of striations on the enamel surface of Primate teeth, either on the buccal surface or on occlusal wear facets, has been attributed to the effect of abrasive particles scratching the enamel during food processing or other dental functions (Ungar et al., 1995; Teaford and Lytle, 1996). Silica-based phytoliths, present in high concentrations in plant materials, are likely to be

responsible for many of these striations and pits (Lalueza et al. 1996; Lucas and Teaford,

Grant sponsor: Spanish MEC; Grant numbers: DGICYT PB-93-0066, DGICYT PB-93-0021.

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Received 9 December 1997; accepted 10 December 1998.

1995; Ungar and Teaford, 1996). Sand, dust (Ungar et al., 1995), and ashes are also potential abrasives (Pérez-Pérez et al., 1994; Lalueza et al., 1996) that may be incorporated in the food during food processing (grinding, air-drying, etc.) or cooking or by direct manipulation of plants and fibers. The anterior teeth (Ungar, 1990, 1992, 1994a,b) may be more prone to the effects of cultural activities involving tooth use than the posterior dentition. Dietary-related enamel scratching and pitting have been shown to be dependent on the type and consistency of the food eaten and on the amount of abrasive particles incorporated in it, both on occlusal wear facets of nonhuman primates (Teaford, 1994; Teaford and Glander, 1991; Ungar, 1992, 1994a; Ungar and Teaford, 1996) and on the buccal surface of both human (Puech and Pant, 1980; Pérez-Pérez et al., 1994; Lalueza and Pérez-Pérez, 1993; Lalueza et al., 1993, 1996) and nonhuman teeth (Ungar and Teaford, 1996).

THE SIMA DE LOS HUESOS SITE: HISTORICAL BACKGROUND

The site of Sima de los Huesos (SH) is located inside the Cueva Mayor/Cueva del Silo cave system, approximately 0.5 km south of the entrance to Cueva Mayor (Fig. 1a), which is found in a rift in the Sierra de Atapuerca southern slope. The entrance to Cueva Mayor becomes a large interior chamber called El Portalón. On the way to the site of Sima de los Huesos from El Portalón, there is an extraordinary large chamber with a very high roof that leads to a junction with three other galleries. One of these galleries (Galería Baja) ends in the site of Sima del Elefante, at the railway cutting known as La Trinchera. This is close to the Galería Complex and Gran Dolina sites, which are currently not connected to the Cueva Mayor/Cueva del Silo caves system and could represent separate systems. Galería has yielded two Middle Pleistocene human remains, and in Gran Dolina nearly 80 human fossil remains have been recovered from Lower Pleistocene levels. They represent the earliest human fossils found in Europe (Carbonell et al., 1995) so far.

A second gallery (Galería del Silo) leads to the Sima de los Huesos site through a crawl-

ing passage that opens into the large chamber called Sala de los Cíclopes (Fig. 1b). The southern half of Sala de los Cíclopes was completely filled by sediments that were later largely washed out in an erosive phase of the karst history. A steep slope of sediment in the southeast corner of Sala de los Cíclopes leads to a flattened terrace of sediment and to the Sima de los Huesos pit. At the base of the 13 m deep shaft, a narrow, blind passage turns west towards the Sala de las Oseras, but at a lower level. The site of Sima de los Huesos is divided in two parts: a proximal one (starting at the bottom of the shaft) with a very steep floor, named the Ramp, and a distal one (to the end of the passage) with a more horizontal floor, called the Chamber. In the roof, almost at the end of the passage connecting the Ramp with the Chamber, there is a vertical conduit that narrows upwards and finally becomes obstructed by limestone blocks.

The Sima de los Huesos site contains a bone-bearing breccia with clayish matrix (Fig. 1c) mainly composed of *Ursus deningeri*, with a minimum number of individuals (MNI) of 166, as well as *Vulpes vulpes* (MNI = 23), and a few remains of *Panthera leo* cf. *fossilis* (MNI = 3), *Panthera* sp. (MNI = 1), *Lynx pardina spelaea* (MNI = 2), *Felix silvestris* (MNI = 1), *Canis lupus* (MNI = 1), *Martes* sp. (MNI = 3), and a small mustelid (MNI = 2) (García et al., 1997). All these animal skeletal elements are mixed in the SH site with more than 1,600 human remains (Arsuaga et al., 1997) belonging to at least 32 individuals (Bermúdez de Castro and Nicolás, 1997). The thickness of the breccia and the amount of fossils increase from the base of the shaft towards the end of the passage. Few fossils are found in the SRA test trench (Fig. 1c). Maximum thickness of the breccia is found at excavation area B (Fig. 1c), where the bottom of the deposit has not yet been reached, and it becomes very thin at the distal excavation squares in area A (Fig. 1c). There are no discontinuities in the human fossil deposit. The fossil-bearing breccia in areas SRM and SRB is similar to that from areas A and B (Fig. 1c), showing in all areas a similar composition of the fossil species represented. The human fossils in SH probably do

not show a clear sorting or alignment, although the study of the main orientations of the fossils has not yet been finished. In the site, there are associations between different bones of the same individual and parts of the same bones, which is not compatible with long postmortem transport. For instance, Cranium 5 was found disarticulated (because the neurocranial structures were open and the face was apart), but all the pieces laid very close to each other at squares U-15/16 (i.e., almost at the end of the cavity). The mandible of this skull was found just below the cranium the following year. Also, a complete pelvis was found in squares U-14/15. Therefore, major postmortem transportation of fossil remains within the clay is unlikely, and only short transportation along the Ramp, with some mixing and dispersal of bones, may have happened.

A sample of human and bear bones from Sima de los Huesos has been directly dated by Bischoff et al. (1997) by U series and electron spin resonance (ESR), indicating a minimum age of about 200 ky and a probable age of >300 ky for the human fossils. These dates are compatible with the faunal content of the site in terms of both large mammals (García et al., 1997) and micro-mammals (Cuenca-Bescós et al., 1997). In 1976, T. Torres discovered the first human fossils in Sima de los Huesos while sampling disturbed sediments for fossil bears. In 1983, in a small sample of disturbed sediment, three human teeth were found among many bear remains. The systematic removal of disturbed sediments began during the 1984 season. In that year and also in 1985, besides the evacuation of debris, bear and human fossils were found in situ in the SH distal excavation squares. During the 1986–1988 field seasons, the excavation of disturbed sediments from SH continued. This disturbed sediment included a mass of mud and bones (mostly bears') mixed with many big, fallen blocks and limestone. The mud and bone mass was taken out to the mouth of Cueva Mayor in backpacks and then transported by car to the Arlanzón River, where it was dried, sieved, and finally sorted by taxa in the laboratory. Many teeth and fragmentary human bones were recovered among thousands of carnivore fragments. In

the 1989 field season, this job was completed, and excavation of undisturbed sediments began, yielding in situ human fossils in the grid squares in area A (Fig. 1c).

In 1990, the excavation continued in undisturbed sediments at area A and preliminary excavations started at area B. In the 1976 field season, Torres had sieved the area close to the top of the shaft for fossils and left the refuse in a hole in the floor. In the 1990 and 1991 field seasons, the debris left by Torres in 1976 was screened, yielding 161 new human fossils. From 1991–1994, area B was excavated, and in 1995 both areas A and B were excavated and connected. Test trenches were excavated in the Ramp at SRA and SRM in 1992 and 1993 and at SRB from 1992–1996. Up to the 1996 campaign, the SH site has yielded more than 300 teeth belonging to a minimum of 32 individuals (Bermúdez de Castro and Nicolás, 1997), found both in disturbed and in situ sediments, either isolated or included in a mandibular or maxillary alveolus.

POPULATION AND METHODS

Buccal microwear analysis of Sima de los Huesos

The large sample of teeth available from Sima de los Huesos provides an excellent opportunity to test the hypotheses proposed by Pérez-Pérez (1990) and Pérez-Pérez et al. (1994) about dietary analysis of human fossil remains using the buccal striation pattern. The dietary attribution of isolated fossil specimens has been attempted for Gibraltar 2 (Lalueza and Pérez-Pérez, 1993) and Banyoles (Lalueza et al., 1993). The interpopulation variability of the buccal striation pattern of modern hunter-gatherer populations (Lalueza et al., 1996) has also been used to characterize the diet of isolated human fossil remains such as Montmaurin, Broken Hill, La Chaise, Malarnaud, Saint Césaire, Marillac, La Quina V, Amud 1, Tabun 1, Tabun 2, Skhül 4, Qafzeh 9, Cromagnon 4, La Madelaine, Rond du Barry, Veyrier sous Saleve, and Abri Pataud (Lalueza et al., 1996). However, these fossil remains are not representative of biological populations since they are usually isolated specimens. Grouping of remains under discrete categories, such as Middle Pleistocene

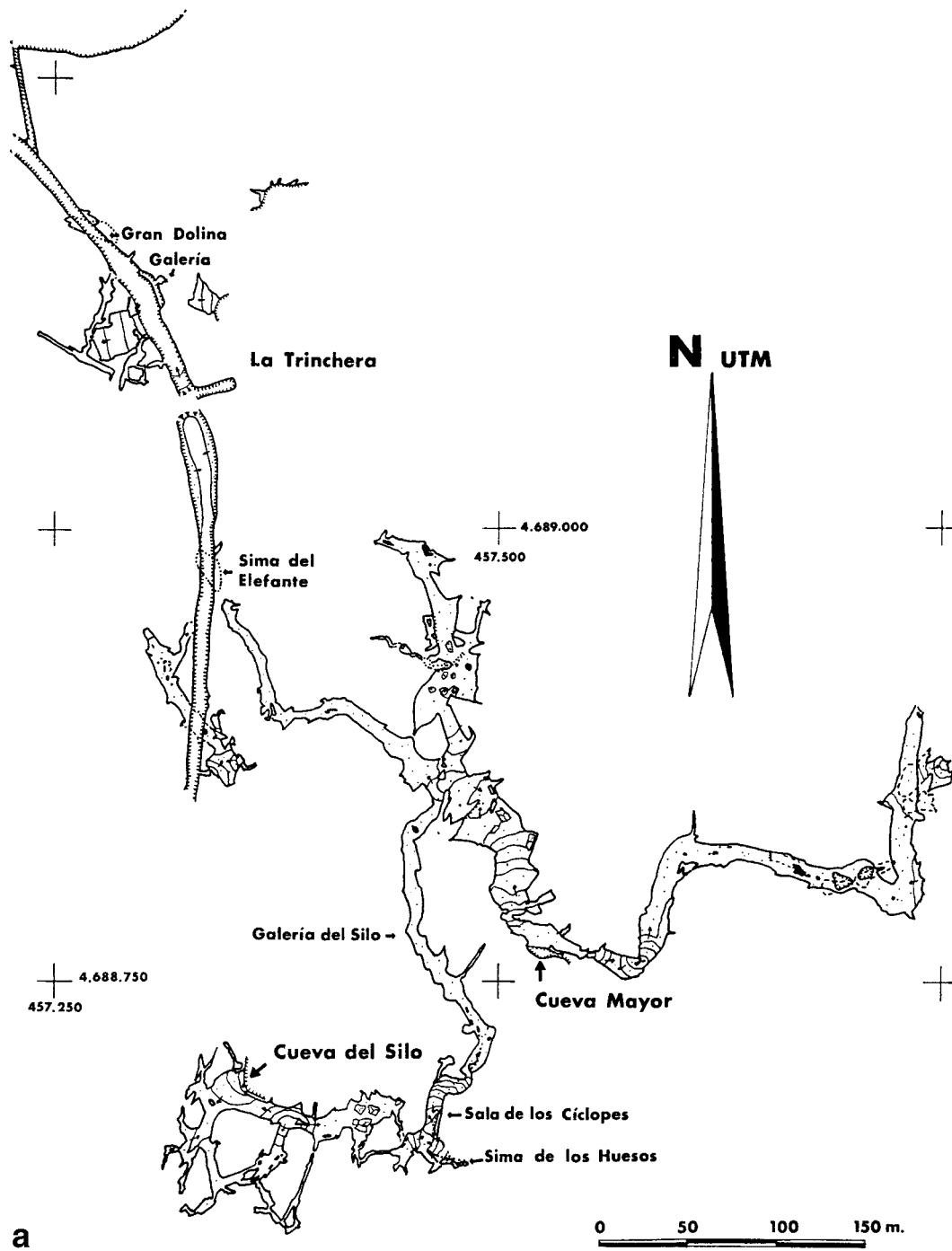
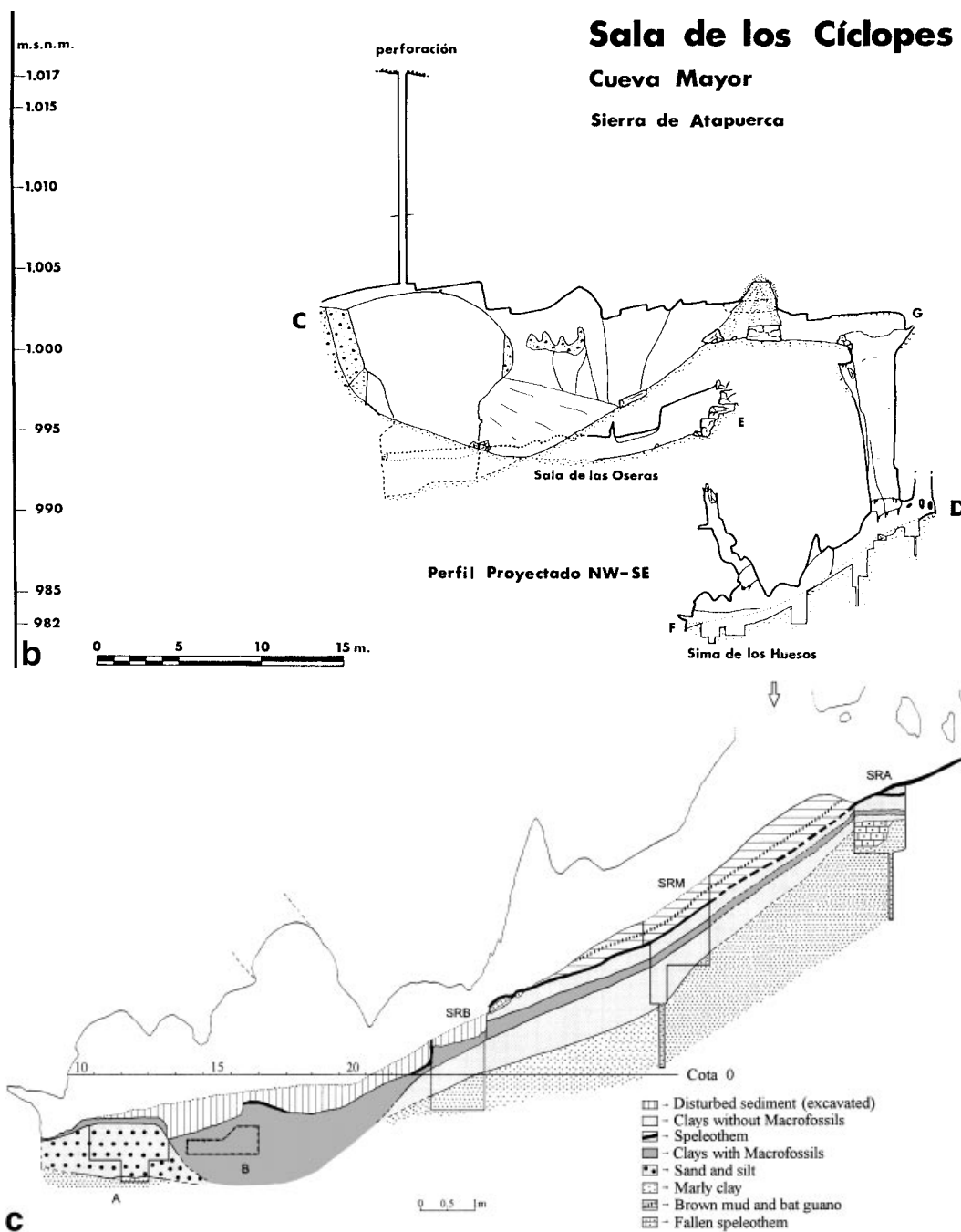


Fig. 1.



or Lower, Middle, and Upper Paleolithic, frequently provides artificial groups, too heterogeneous both geographically and temporally to be considered representative of distinct biological populations. However, the human remains recovered from Sima de los Huesos have been suggested to represent a biological population (Bermúdez de Castro and Nicolás, 1997) derived from a single geologic sedimentary event (Arsuaga et al., 1997) dating to 300,000 BP (Bischoff et al., 1997). In the present study, we analyze the intrapopulation variability of the buccal striation pattern in a sample of teeth recovered from Sima de los Huesos till the 1995 field campaign. The main objective of this analysis is to test the hypotheses stated in previous studies with modern populations regarding the intra- and interindividual homogeneity of the striation pattern observed in the buccal surface of the postcanine teeth (Pérez-Pérez, 1990; Pérez-Pérez et al., 1994). Special focus is on the feasibility of making inferences about dietary behavior from buccal microwear in relation to environmental constraints, climatic conditions, the type of food available, dietary specialization, and food-processing techniques. If the intrapopulation variability in the fossil sample from Sima de los Huesos is not dependent on the analyzed tooth, intragroup differences, if found, might be indicative of differences in dietary habits. The tooth sample from Sima de los Huesos is, along with that from Krapina (Freyer and Russell, 1987; Lalueza and Freyer, 1997), the largest Lower Paleolithic tooth collection available where individual, sex, and age group classification may be carried out. The analysis of its buccal striation pattern and its comparison with that of modern hunter-gatherer populations (Lalueza et al., 1996) will help to determine whether the dietary striation pattern of such modern groups may be applied to the characterization of the diet of fossil hominid species whose diet and food-processing techniques were probably not so elaborate and refined. In addition, the analysis of the SH microwear will contribute to future studies about the characterization of the intra- and interspecific variability of the striation pattern of both human and nonhuman Primate species.

The sample

The buccal surface microwear striation pattern of human postcanine teeth (Pm3, Pm4, M1, M2, and M3) retrieved from the site of Sima de los Huesos (Sierra de Atapuerca, Burgos, Spain) was analyzed. The anterior teeth (I1, I2, C) were not considered in the present dietary analysis, although incisor microwear studies have significantly contributed to understanding diet and feeding behavior in primates (Walker, 1976; Ungar, 1992, 1994a,b). The teeth recovered in the 1976–1995 field seasons are included in this study. They are curated at institutions in both Burgos and Madrid. The remains recovered between 1976 and 1987 are stored at the Museo Paleontológico in Burgos, and the materials recovered from 1988 on are curated at the Department of Paleobiology, Museo Nacional de Ciencias Naturales, (by J.M. B. de C.), and at the Department of Paleontology, Facultad de Ciencias Geológicas (by J.L.A.), both in Madrid. Plastic casts of the teeth were made by A. P.-P. in Madrid (1994, 1996) and Burgos (1995) following procedures detailed below. The casts were micrographed and analyzed during 1996, and in 1997 repeated casting was made for some teeth in order to maximize the sample size. New casts were also obtained for some of the teeth recovered in the 1996 campaign. Teeth from the 1996–1998 field seasons, both from Sima de los Huesos (300,000 BP) and Gran Dolina (850,000 BP), are being processed at present.

A total of 217 molar teeth had been recovered from the Sima de los Huesos site through the 1996 field season: 28 Pm3, 38 Pm4, 52 M1, 51 M2, and 48 M3 (Table 1). The minimum number of individuals (MNI) in the site of Sima de los Huesos would be 20 if only isolated teeth were considered ($n = 20$ for left M_1 's). However, teeth were assigned to specific individuals on the basis of 1) their inclusion in maxillary or mandibular bone fragments, 2) coincidence of proximal and/or distal crown wear facets between adjacent teeth, 3) the degree and continuity of occlusal wear, and 4) similarity in tooth size and morphology. Thus, the MNI has been established at 32 individuals (Bermúdez de Castro and Nicolás, 1997). Age at

TABLE 1. Sample sizes of permanent, posterior teeth (Premolars, Molars) studied from Sima de los Huesos (Sierra de Atapuerca, Spain)¹

Jaw	Side	Sample	Pm3		Pm4		M1		M2		M3		All	
			n	%	n	%	n	%	n	%	n	%	n	%
Mandible	Left	Teeth	9	—	13	—	20	—	12	—	12	—	66	—
		Casts	8	89	11	85	20	100	12	100	11	92	62	94
		Images	6	67	8	62	13	65	9	75	8	67	44	67
		High	0	—	1	—	2	—	2	—	0	—	5	—
	Right	Normal	6	67	7	54	11	55	7	58	8	67	39	59
		Teeth	10	—	13	—	13	—	16	—	15	—	67	—
		Casts	9	90	10	77	13	100	13	81	12	80	57	85
		Images	6	60	9	69	12	92	9	56	5	33	41	61
		High	0	—	0	—	4	—	1	—	1	—	6	—
		Normal	6	60	9	69	8	62	8	50	4	27	35	52
		Teeth	4	—	4	—	6	—	9	—	8	—	31	—
		Casts	4	100	4	100	5	83	8	89	8	100	29	93
		Images	2	50	3	75	4	67	3	33	0	0	12	39
		High	0	—	0	—	0	—	0	—	0	—	0	—
		Normal	2	50	3	75	4	67	3	33	0	0	12	39
Maxila	Left	Teeth	4	—	4	—	6	—	9	—	8	—	31	—
		Casts	4	100	4	100	5	83	8	89	8	100	29	93
		Images	2	50	3	75	4	67	3	33	0	0	12	39
		High	0	—	0	—	0	—	0	—	0	—	0	—
	Right	Normal	2	50	3	75	4	67	3	33	0	0	12	39
		Teeth	5	—	8	—	13	—	14	—	13	—	53	—
		Casts	5	100	8	100	9	69	11	79	8	62	42	79
		Images	5	100	5	63	6	46	9	64	2	15	27	51
		High	2	—	0	—	0	—	0	—	0	—	2	—
		Normal	3	60	5	63	6	46	9	64	2	15	25	47
		Teeth	28	—	38	—	52	—	51	—	48	—	217	—
		Casts	26	93	34	89	47	90	44	86	39	81	190	88
		Images	19	68	25	66	35	67	30	59	15	31	124	57
		High	2	—	1	—	6	—	3	—	1	—	13	—
		Normal	17	61	24	63	29	56	27	53	14	29	111	51

¹ Teeth, number of teeth recovered from the site till the 1996 campaign; casts, number of teeth for which plastic casts were obtained; images, number of teeth for which SEM micrographs were taken; high, number of teeth that showed a high density of scratches; normal, number of teeth that could be analyzed for the intrapopulational variability. Of the 217 available teeth, 190 (87.6%) were casted, but undamaged tooth surfaces and high-quality SEM images could be obtained only for 154 (57.1%) teeth, 11 of which had a high density of striations and 111 (51.2%) had normal striation densities.

death of individuals was determined based on tooth-eruption tables for deciduous and permanent dentitions. Three categories of age were considered for the present study based on the age classification made by Bermúdez de Castro and Nicolás (1997): 12–17, 18–24, and 25–40 years old. Sex was estimated from the analysis of the pattern of sexual dimorphism in size and shape present in the mandibular bone of Sima de los Huesos (Rosas, 1995) and from the size variation of teeth within sexed mandibles (Bermúdez de Castro et al., 1993; Bermúdez de Castro and Nicolás, 1997). A clear pattern of sexual dimorphism in both size and shape seems to emerge from the analysis of the mandibles recovered from the SH site (Rosas, 1995). This pattern has been used to estimate the sex of the 14 individuals who were identified by their mandibles and teeth. On the other hand, a great size variability has been pointed out from first observations of the SH dental sample (Bermúdez de Castro, 1986, 1993; Bermúdez de Castro et al., 1993). The dental crown dimensions of

some individuals from SH gather on the lower and upper zones of their respective distributions (see Bermúdez de Castro and Nicolás, 1997). This is the case for individuals VII, VIII, XII, and XX, who have very big teeth, and for individuals, III, X, XI, and XIX, whose teeth are the smallest. This peculiar crown size distribution is responsible for the high values of variances and coefficients of variation seen in the lower canines and third premolars and upper second molars, which are significantly higher (F-test) than those of a modern human sample (Bermúdez de Castro and Nicolás, 1997). Since the SH sample is likely to represent the same biological population, the most reasonable interpretation of these results is that factors related to sex affect to a greater extent the dental size variability of the SH hominids. Thus, the first approach is to consider that the biggest teeth of the SH sample probably belong to males and the smallest ones probably to females. Individuals VIII and XX, who are not represented by mandibular remains, may then be males,

whereas individual XI, who has the smallest teeth, is tentatively designated a female.

Tooth casts and image processing

Plastic casts were obtained of 190 (87.6%) permanent cheek teeth (26 Pm3, 34 Pm4, 47 M1, 44 M2, 39 M3), out of the 217 teeth available (Table 1). Tooth casts of the central third (between the cervical and occlusal thirds) of the buccal surface of the postcanine teeth were obtained with Triafol plastic (Balzers Union, Balzers, FL) dissolved in chloroform (for a detailed methodological description see Pérez-Pérez 1990; Pérez-Pérez et al. 1994) on the central portion of the premolars (Pm3 and Pm4) and on the proximal half of the molars (M1, M2, and M3). All the casts were sputter-coated with 400 Å of gold and observed in secondary mode with a Hitachi scanning electron microscope (SEM), nearly perpendicular to the electron beam. Buccal surfaces that showed no casting defects or postmortem damage (Teaford, 1988) were micrographed at $\times 100$ magnification, and only images lacking any type of casting or enamel defect or picture deficiencies (lights or shadows, etc.) were processed. Thus, the final analyzed sample consists of 124 teeth, 57.1% of all available teeth, and 65.3% of all casts taken (Table 1).

The negative micrographs measured 69 mm (horizontal) \times 49 mm (vertical) and included a 500 μ m scale line for calibration. An approximately square surface (44.0 mm horizontal \times 45.7 mm vertical) of the negative picture was scanned with an Epson 8000 scanner at 300 dpi resolution and 256 gray tones, obtaining an 8 bit digitized image with 520 pixels horizontal \times 540 pixels vertical, which was saved in a TIFF file format. The scanned surface was not square due to limitations on the proportions allowed by the scanning software (Epscan version 1.0 for the Epson 8000). The 500 μ m scale encompassed an average of 354 pixels after repeated measurements, which represents 1.4124 μ m/pixel for the linear calibration of the image. Thus, the actual enamel area included in the scanned surface was 0.56 mm² (560,160.551808 μ m²; 734.448 μ m horizontal \times 762.696 μ m vertical). This studied surface is the same surface indicated in our previous publications, which was improv-

erly referred to as approximately 1 mm². Actual size was not exactly estimated then because the image analysis system that was used (IBAS 2 image analysis system) did not require scanning because the negative image was captured with a high resolution videocamera and directly processed without digitalization. In the present study, the image was scanned at 300 dpi covering exactly the same vertical dimension of the negative as in previous studies. Thus, the two procedures are identical with approximately the same area, except for the fact that the scanned image is not exactly square.

The scanned images were processed with Adobe (Mountain View, CA) Photoshop (version 2.5) in order to remove shadows and expand the gray levels in the same way that was previously done with the IBAS 2 system. The high pass Photoshop filter was applied to "remove shading by retaining the areas where sharp color transitions occur and suppressing the rest of the image," as the filter "emphasizes very bright areas and highlights, and removes low-frequency detail in an image" (Photoshop version 2.5 online manual). A 50 pixel radius around the image edges was used in order to retain part of the pixels adjacent to the edge pixels. The value of 50 was chosen after multiple trials until similar results were obtained in comparison to the IBAS 2 methodology previously used. Then the levels of gray tones were rescaled automatically by "defining the lightest and darkest pixels in each channel as white and black, and then adjusting the gray tones in between" (Adobe Photoshop Users Guide). Image enhancement may have a significant effect on striation width. However, at $\times 100$ magnification, striation width cannot be measured. The enhanced images obtained were analyzed with the Sigma Scan Image™ software (version 1.2; Jandel Scientific, Corte Madera, CA). The length (L) and slope (S) of all striations were automatically measured after defining the beginning and the end of each striation observed in the scanned area. The slope of the scratch was transformed into an angle measure (A) in degrees using the equation $A = \arctg(S \times \pi/180)$. Negative angles were transformed into positive by adding 180° since only angles between 0° and 180° were considered be-

cause the starting point of the scratch cannot be determined at $\times 100$. All striations, including those cut off by the border of the SEM visual field, were measured, and thus average striation length per observed area, rather than actual striation length, was estimated. The variables obtained (length and angle of each striation) are identical to those considered by us in previous studies of the tooth striation pattern on the buccal surface of the molar teeth.

All observed scratches were classified by categories of orientation: horizontal (H) ($0-22.5^\circ$ and $157.5-180^\circ$), vertical (V) ($67.5-112.5^\circ$), mesio-occlusal to disto-cervical (MD) ($22.5-67.5^\circ$ on the upper left and lower right teeth and $112.5-157.5^\circ$ on the lower left and upper right teeth), and disto-occlusal to mesio-cervical (DM) ($22.5-67.5^\circ$ on lower left and upper right teeth and $112.5-157.5^\circ$ on upper left and lower right teeth). Each one of the four groups defined (H, V, MD, DM) covers a range of 45° . From the measurements of length (L) and orientation angle (A), summary statistics of striation number (N), length (X), and variability (S) of the length were obtained by categories of orientation for each analyzed tooth. Thus, 15 variables were derived: five measuring the average density of striations by orientation (NH, NV, NMD, NDM, and NT for the total number), five measuring the average length of the striations (XH, XV, XDM, XMD, and XT), and five measuring the standard deviation of the length, also by orientation groups and for all the striations (SH, SV, SDM, SMD, and ST). The buccal striation pattern of a population may then be characterized by summary statistics of these 15 derived variables (for detailed descriptions see Pérez-Pérez et al., 1994; Lalueza et al., 1996). Such summary variables are likely to follow normal distributions since they are average values obtained from original variables (Sokal and Rohlf, 1981). Normality tests of the variables were done using Kolmogorov-Smirnov goodness of fit tests. The usefulness of parametric factorial ANOVA and discriminant analyses for characterizing the intrapopulation variability of this derived variables has already been discussed (Pérez-Pérez et al., 1994; Lalueza et al., 1996). The intragroup and intergroup comparisons were

done with one-way analyses of variance, with the Bonferroni adjustment when multiple significant tests were done, and multivariate factorial and discriminant analyses with SPSSTM (version 6.1.3 for WindowsTM). Ranked data tests greatly limit the power of analysis, and their use is not justified since normality of distributions is the rule. Factorial ANOVA was used to test for differences among groups defined by the factors of age (subadult and adult), sex (female and male), maxilla (lower and upper), side (left and right), and tooth (Pm3, Pm4, M1, M2, and M3). The discriminant analyses were used to determine if dietary-related differences between groups could be discriminated and to make group classification of ungrouped specimens using the discriminant functions derived from the analyses.

RESULTS

High-density micrographs

The SEM micrographs obtained showed a highly dispersed pattern of number of striations (NT) per surveyed area, ranging from 102 to 522 in the total sample ($n = 138$). However, almost 90% of all micrographs had between 100 and 300 striations, whereas some ($n = 15$) showed higher numbers (Table 2). Overall observation of these micrographs allowed for a clear distinction of unexpected highly striated enamel surfaces characterized by a high density of generally short striations. One-way analyses of variance (Table 2) between this group and the rest of the sample ($n = 123$) showed significant differences for nine of the 15 variables considered, including the average number of striations (NT, NV, NH, NDM, NMD) and their average length (XT, XV, XDM, XMD). No differences were observed for the average length of the horizontal striations (XH) or for the lengths' dispersions (ST, SV, SH, SDM, SMD). Since such a high density of striations could be caused by factors other than dietary-related ones, all micrographs were classified into one of two categories of striation density (normal and high). The normal-density group was defined as having a pattern of striations comparable to that present in other previously studied populations (Pérez-Pérez, 1990; Pérez-Pérez et al.,

TABLE 2. Micrographs of teeth from *Sima de los Huesos* having a high striation density¹ and summary statistics and one-way ANOVA comparisons between the normal and high density samples

High-density sample							
Tooth	Individual number	Sex	n/N ²	NT ³	Tooth	Maxillae	Side
AT-75	VI	Female	1/2	327	M2	Mandible	Left
AT-147	VII	Male	2/9	322	Pm4	Mandible	Left
AT-21	VII	Male	2/9	340	M1		
AT-141	X	Female	1/2	338	M1	Mandible	Right
AT-300	XII	Male	1/6	313/305	M1	Mandible	Right
AT-272	XIV	?	1/2	396	M1	Mandible	Right
AT-22	XV	?	2/3	309	M1	Mandible	Left
AT-101	XV	?	2/3	320	M1	Mandible	Right
AT-101	XV	?	2/3	522	M1	Mandible	Right
AT-823	XVII	?	1/2	312	Pm3	Maxila	Right
AT-505	XIX	Female	1/2	407	M2	Mandible	Left
AT-589	XX	Male	1/7	312	Pm3	Maxila	Right
AT-605	XXII	Male	1/5	370	M2	Mandible	Right
AT-604	XXV	Female	1/3	306	M3	Mandible	Right

Normal-density sample (n = 123)					High-density sample (n = 15)				One-way ANOVA	
	Mean	σ	Minimum	Maximum	Mean	σ	Minimum	Maximum	F	P
NH	22.44	12.09	4	75	53.60	19.53	23	92	76.17	0.0000
NDM	33.93	16.02	9	109	68.93	27.09	25	134	53.55	0.0000
NMD	41.80	19.47	11	123	88.20	31.60	48	156	64.98	0.0000
NV	76.98	25.05	23	146	135.87	18.41	107	183	77.55	0.0000
NT	175.16	42.53	102	284	346.60	58.27	305	522	199.26	0.0000
XH	93.97	29.73	42.50	192.78	82.31	24.85	47.74	122.37	2.12	0.1474
XDM	87.78	27.96	42.29	185.26	71.38	12.17	50.16	97.82	5.02	0.0267
XMD	86.93	23.34	35.91	185.10	71.09	13.36	54.12	93.87	6.62	0.0112
XV	99.37	21.14	36.85	156.73	86.42	20.09	50.84	126.65	5.07	0.0259
XT	95.30	17.92	50.70	145.42	80.20	13.38	54.73	106.14	10.16	0.0018
SH	80.45	39.67	17.54	191.03	76.63	32.48	25.92	152.61	0.13	0.7241
SDM	80.18	40.74	20.52	216.08	70.58	20.91	32.88	98.05	0.80	0.3714
SMD	80.47	34.42	17.59	199.20	69.74	18.09	43.79	108.42	1.40	0.2384
SV	90.56	27.15	17.18	163.97	84.27	26.68	43.80	150.70	0.72	0.3973
ST	92.18	22.40	46.44	166.87	81.50	18.23	45.01	115.73	3.15	0.0782

¹ Striation density classification was done previous to the image analysis.² n/N, number of teeth with a high density of striations (n) over total number of teeth studied of the same individual (N).³ NT, total number of striations observed for the specified tooth.

1989, 1994; Lalueza et al., 1996) with mainly vertical and usually long striations.

The high-density group showed a high number of randomly oriented and short striations. This group included 15 casts (Table 2) taken from 13 teeth belonging to 11 individuals. All the variables analyzed for the high-density group follow normal distributions (no significant Kolmogorov-Smirnov Z values were found at the $\alpha = 0.05$ confidence level). The high-density teeth show a range of total number of striations (NT) between 305 and 522 ($\bar{x} = 346.60$, $\sigma = 58.27$, $n = 15$), whereas the normal-density group ($n = 123$) has a range between 102 and 284 ($\bar{x} = 175.16$, $\sigma = 42.53$). Figure 2 shows six micrographs of teeth with high and normal scratch densities. Their striation patterns are clearly distinct, and the high-density

group has more but also shorter striations (between 54.73 and 106.14 μm long) than the normal one (between 50.70 and 145.42 μm) for all orientations. The significantly smaller average value of the length of striations in the high-density group is due to smaller maximum length values rather than to smaller minimum values (Table 2). Separate analyses of these two groups are advisable until the nature of such differences can be ascertained.

Intrapopulation variability of the normal-density sample

The analysis of the intrapopulation variability of the buccal striation pattern was done only with the normal-density group, since high striation densities may not be dependent only on dietary habits, as will be

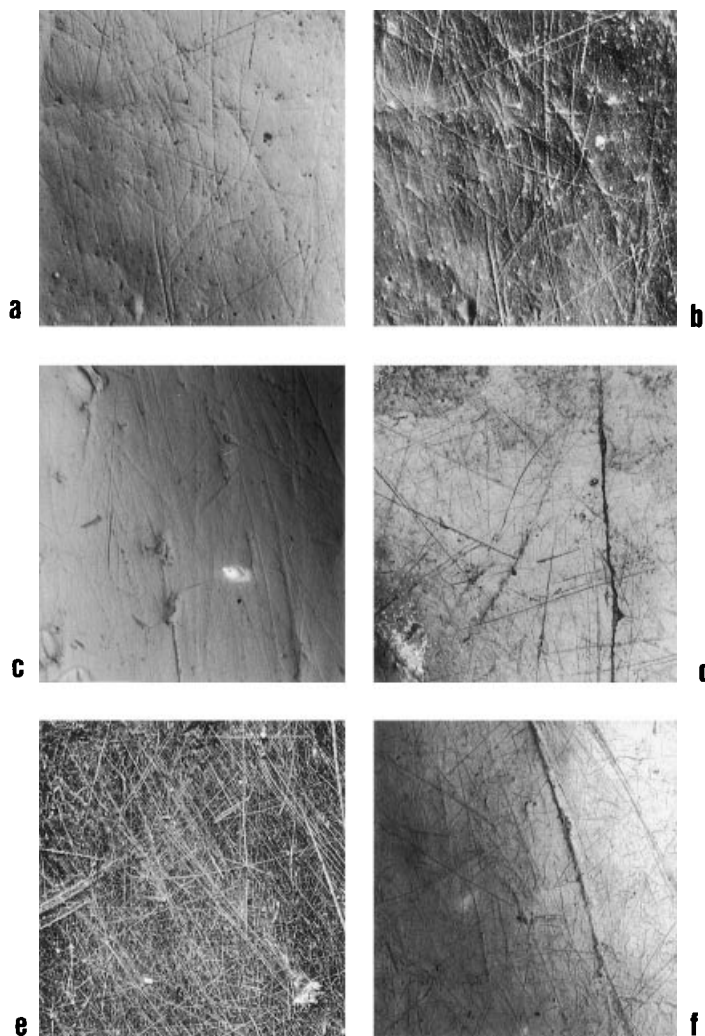


Fig. 2. SEM micrographs of normal (a–c) and high-density (d–f) buccal tooth enamel surfaces. **a:** AT-26, micrograph number 4331 ($n = 200$). **b:** Same as panel a with image enhancing. **c:** AT-279, micrograph 0404 ($n = 148$). **d:** AT-22, micrograph 8472 ($n = 308$). **e:** AT-505, micrograph 0405 ($n = 407$). **f:** AT-101, micrograph 8474 ($n = 522$). Numbers in parentheses indicate the number of striations observed in each image. Normal and high-density micrographs can be clearly distinguished.

discussed later. One micrograph per studied tooth was selected for analysis from the normal-density group. Duplicate micrographs of teeth at different enamel positions were discarded, obtaining a final sample of 111 teeth (Table 1). Normality tests of the 15 variables showed only one significant deviation from normality (variable NH) in this group (Kolmogorov-Smirnov $Z = 1.6567$, $P = 0.0083$). The number of horizontal striations has also been shown to deviate from normality in previously studied populations (Lalueza et al., 1996). Summary statistics of the variables studied by factors are not shown because of space limitations. The

factors considered for the intrapopulation variability analysis were jaw (mandible, maxilla), sex (female, male), tooth (Pm3, Pm4, M1, M2, M3), side (left, right), tooth position in the alveolus (in situ, isolated), type of sediment (disturbed, in situ), and postrecovery cleaning and storage conditions (unknown, good, excellent). The factors of position, sediment, and treatment are indicative of depositional and recovery conditions of the teeth from Sima de los Huesos. The in situ teeth were found in their alveoli, either in the mandible or in the maxilla, irrespective of whether the bone was complete (mandible or skull) or fragmented. The

TABLE 3. One-way analyses of variance of the normal-density sample ($n = 111$) for the 15 variables measured, by categories of grouping factors¹

	NT/XT/ST		NH/XH/SH		NV/XV/SV		NMD/XMD/SMD		NDM/XDM/SDM	
	F	P	F	P	F	P	F	P	F	P
Jaw	12.9768	0.0005*	8.2141	0.0050*	0.0362	0.8495	14.5644	0.0002*	3.6908	0.0573
	1.8545	0.1761	0.1433	0.7058	1.1831	0.2791	0.4894	0.4857	2.0674	0.1533
	4.5845	0.0345*	0.3019	0.5838	3.2225	0.0754	2.1040	0.1498	3.5746	0.0613
Tooth	0.6999	0.5937	1.9729	0.1039	1.5710	0.1874	0.6361	0.6379	1.1823	0.3229
	1.6505	0.1670	0.6747	0.6110	1.2008	0.3148	2.3898	0.0554	1.5236	0.2006
	0.6688	0.6150	0.5247	0.7178	0.6590	0.6218	1.2280	0.3040	1.1131	0.3543
Side	0.2852	0.5944	0.4202	0.5182	0.0154	0.9015	0.3329	0.5651	0.1280	0.7212
	2.0754	0.1526	1.6633	0.1999	1.4469	0.2316	0.4557	0.5011	1.6457	0.2023
	0.6966	0.4058	2.2674	0.1350	0.0918	0.7625	0.3780	0.5400	0.9268	0.3378
Position	1.4352	0.2335	1.6411	0.2029	0.2366	0.6276	0.4166	0.5200	0.2890	0.5920
	11.9785	0.0008*	6.7937	0.0104*	6.4563	0.0125*	1.5394	0.2174	9.9874	0.0020*
	10.1538	0.0019*	3.2893	0.0725	5.3478	0.0226*	0.2243	0.6367	8.2588	0.0049*
Sediment	0.9681	0.3273	0.5137	0.4751	0.2911	0.5906	0.0335	0.8551	0.8531	0.3577
	0.3575	0.5511	1.5560	0.2149	0.0439	0.8344	0.0098	0.9214	0.3060	0.5813
	5.8455	0.0173*	2.9181	0.0904	2.3250	0.1302	1.8860	0.1725	1.7736	0.1857
Treatment	1.9028	0.1541	0.6178	0.5410	0.7596	0.4704	0.4751	0.6231	0.8075	0.4486
	2.5006	0.0868	0.8262	0.4404	2.3979	0.0957	1.1700	0.3143	1.3745	0.2574
	0.3474	0.7073	0.3717	0.6904	0.1934	0.8244	0.0281	0.9723	0.0085	0.9915
Age	0.4652	0.6296	1.4254	0.2460	0.0635	0.9385	1.2356	0.2957	1.0088	0.3689
	2.5175	0.0865	0.7316	0.4841	2.3173	0.1046	0.9709	0.3828	0.2060	0.8142
	3.3587	0.0393*	2.1250	0.1256	2.7659	0.0685	1.1384	0.3251	0.2965	0.7442
Sex	2.6059	0.1104	0.8926	0.3476	1.5525	0.2164	0.0304	0.8620	1.9640	0.1649
	4.7460	0.0323*	3.0382	0.0851	0.3259	0.5697	2.8225	0.0968	12.8182	0.0006*
	4.6730	0.0336*	1.3323	0.2518	0.0406	0.8409	0.3605	0.5499	15.9008	0.0001*
Sex and maxila	4.0626	0.0097 3-2	4.2406	0.0078*	0.8493	0.4711	2.6463	0.0547	1.5614	0.2053
	2.993	0.0838	1.2272	0.3054	0.5622	0.6415	1.5718	0.2028	5.5792	0.0016 3-1,2
	2.6806	0.0525	0.4440	0.7222	0.6142	0.6078	0.5015	0.6823	6.8859	0.0004 3-1,2
Sex and age	0.8569	0.5141	0.9299	0.4665	1.4906	0.2027	0.9385	0.4610	1.0649	0.3864
	2.9606	0.0169 6-2	1.4828	0.2052	1.2527	0.2931	2.2219	0.0605	3.4137	0.0077 6-3
	3.7751	0.0041 6-2,1	1.7555	0.1321	1.3916	0.2368	1.4585	0.2132	4.4829	0.0012 6-1,3
Sex, maxila, and position	2.1214	0.0604	2.3133	0.0418*	0.7947	0.5769	1.5526	0.1728	2.1334	0.0590
	1.5220	0.1824	1.5667	0.1685	0.6351	0.7017	0.9552	0.4613	3.3933	0.0051 7-1,5
	1.5873	0.1624	0.9859	0.4409	1.3672	0.2387	0.7588	0.6045	3.7830	0.0024 7-1,2,5

¹ The grouping factors are as follows: jaw (mandible and maxila); tooth (Pm3, Pm4, M1, M2, M3); side (left, right); position (in situ, isolated); sediment (disturbed, in situ); treatment (unknown, good, excellent); age (12–17, 18–24, 25–40); sex (male, female); sex and maxila (1, male, mandible; 2, male, maxila; 3, female, mandible; 4, female, maxila); sex and age (1, male, 12–17; 2, male, 18–24; 3, male, 25–40; 4, female, 12–17; 5, female, 18–24; 6, female, 25–40); and sex, maxila, and position (1, male, mandible, isolated; 2, male, maxila, isolated; 3, female, mandible, isolated; 4, female, maxila, isolated; 5, male, mandible, in situ; 6, male, maxila, in situ; 7, female, mandible, in situ).

* Significance of P is shown at confidence levels of $\alpha = 0.05$. Numbers beside the P value are pairwise group t -test comparisons after one-way ANOVA with Bonferroni correction.

disturbed sediments correspond to the upper levels of Sima de los Huesos that might have suffered postdepositional processes, either related to carnivore or bear activities in the cave (Andrews and Fernández, 1997) or to future excavations previous to 1983.

One-way factorial analyses of variance (Table 3) show significant differences (at the $\alpha = 0.05$ confidence level) for some group comparisons. Differences are found between mandibular and maxillary teeth for the total number of striations (NT, $P = 0.0005$), standard deviation of the length of all the striations (ST, $P = 0.0345$), number of horizontal striations (NH, $P = 0.0050$), and number of mesio-distal ones (NMD, $P = 0.0002$). Differ-

ences between in situ and isolated teeth are found for the length of the horizontal (XH, $P = 0.0104$), vertical (XV, $P = 0.0125$), disto-mesial (XDM, $P = 0.0020$), and all the striations (XT, $P = 0.0008$) as well as for the standard deviation of the length of the vertical (SV, $P = 0.0226$), disto-mesial (SDM, $P = 0.0049$), and all the striations (ST, $P = 0.0019$). Significant differences were found for the standard deviation of the length of all the striations between disturbed and in situ sediment (ST, $P = 0.0173$) and between age groups (ST, $P = 0.0393$). Sex-related differences were present for both the average length and the standard deviation of the length of the disto-mesial (XDM, $P = 0.0006$;

SDM, $P = 0.0001$) and all (XT, $P = 0.0323$; ST, $P = 0.0336$) striations. No differences were observed for the factors of tooth, side, and postrecovery treatment (Table 3). These results indicate that intrapopulation differences exist in the buccal striation pattern of the sample of teeth from Sima de los Huesos and that the differences observed are mainly due to differences between jaws, with the maxillary teeth having more striations (NT = 194.86) than the mandibular ones (NT = 166.65), differences between sexes, with females having longer striations (XT = 102.09, XDM = 102.39) than males (XT = 94.44, XDM = 80.72), and differences between tooth positions, with isolated teeth having longer striations (XT = 100.51) than in situ teeth (XT = 90.04). Only slight differences are found for the factors of age and sediment for the ST variable. Significant differences in the one-way ANOVAS are also found (Table 3) for the combined factors of sex and maxilla for variables NT, NH, XDM, and SDM (female mandibular teeth differing from the other groups), of sex and age for variables XT, ST, XDM, and SDM (25–40-year-old females differing from the other groups), and of sex, maxilla, and position for variables NH, XDM, and SDM (female mandibular in situ teeth showing significant differences). Table 3 shows all the significant pair-group comparisons at a 5% confidence level (t -test with Bonferroni correction after one-way ANOVA), indicating which groups are significantly distinct.

Discriminant analysis of teeth and sex classification. Since the factors of sex, maxilla, and position seemed to be responsible for most of the intrapopulation variability observed, a discriminant analysis was done to determine if the eight groups defined by the three combined factors could be clearly discriminated. The groups obtained were as follows: 1) male, mandibular, isolated teeth ($n = 8$); 2) male, maxillary, isolated teeth ($n = 11$); 3) female, mandibular, isolated teeth ($n = 7$); 4) female, maxillary, isolated teeth ($n = 3$); 5) male, mandibular, in situ teeth ($n = 21$); 6) male, maxillary, in situ teeth ($n = 7$); 7) female, mandibular, in situ teeth ($n = 26$); 8) female, maxillary, in situ teeth ($n = 0$) (no micrographs were

available for this group). Group membership probability for the direct test (all 15 variables entering the analysis at the same time) of the discriminant analysis was estimated from the sample sizes instead of using equal probabilities for all groups because most teeth considered belonged to mandibular in situ groups (samples 5 of males and 7 of females). The differences in size between groups are due to deviations in the frequency distribution of the recovered teeth and in the sampling (Table 1). Six discriminant functions were obtained, explaining 35.87%, 24.34%, 20.57%, 11.91%, 5.34%, and 1.97% of the total variance, respectively, with a 75.90% of correct classification probability. The first two functions explained 60.21% of the total variability. Figure 3 shows 95% equiprobable ellipses of the seven groups analyzed for the these first two discriminant functions (labels A–G in Fig. 3 indicate centroids of groups 1–7). Although the ellipses overlap considerably, significant differences are found for the discriminant factors obtained between some of the groups considered. One-way analyses of variance (using Bonferroni correction for between-group comparisons after the ANOVA) of the six functions obtained showed significant differences between some of the groups for four of the six functions derived (data not shown), indicating that significant intergroup variability was present within the sample. A total of 28 ungrouped teeth (without sex attribution) were classified into one of the eight categories considered using the covariance matrices from the discriminant functions obtained. Table 4 shows the probabilities of group membership for the first and second groups with the highest classification probabilities along with the expected groups (named *actual group* in the table) depending on the analyzed tooth. Since groups 1, 2, 5, and 6 are male teeth and groups 3, 4, 7, and 8 female teeth, the probability of a tooth belonging to a given sex was computed as the sum of the probabilities obtained for the groups of that sex. Many of the probabilities of sex assignment obtained for this analysis are above 80% and 90%. As indicated, the overall probability of correct classification derived from this discriminant analysis was 75.90%. This prob-

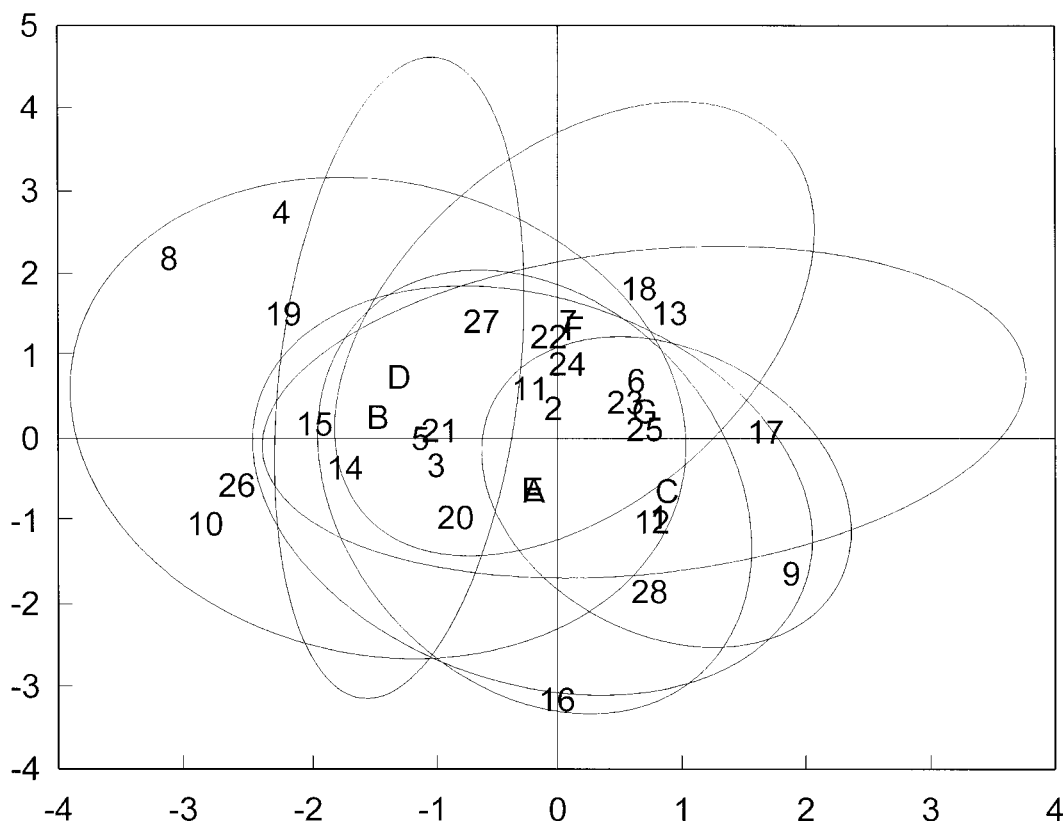


Fig. 3. Ninety-five percent equiprobable ellipses for the first two functions obtained with the discriminant analysis of teeth for the factors of sex, maxilla, and position. Capital letters at the centroids of each ellipse are groups of male, mandibular, isolated teeth (A) ($n = 8$); male, maxillary, isolated teeth (B) ($n = 11$); female, mandibular, isolated teeth (C) ($n = 7$); female, maxillary, isolated teeth (D) ($n = 3$); male, mandibular, in

situ teeth (E) ($n = 21$); male, maxillary, in situ teeth (F) ($n = 7$); and female, mandibular, in situ teeth (G) ($n = 26$). The female, maxillary, in situ teeth group is not represented ($n = 0$). The numbers (1–28) within the ellipses ranges are the ungrouped cases shown in Table 4 classified with the discriminant functions obtained with the first discriminant analysis. X-axis shows discriminant function 1, and Y-axis shows function 2.

ability decreases to 68.67% if the factor of position is not included in the discriminant analysis, only considering the factors of maxilla and sex as grouping variables with four categories: male mandible ($n = 29$), male maxilla ($n = 18$), female mandible ($n = 33$), and female maxilla ($n = 3$). Three discriminant functions are obtained in this case, explaining 61.75%, 34.42%, and 3.84% of the total variance, respectively, which again allow classification of ungrouped cases for sex. The sex classification probabilities obtained with this second discriminant analysis are also shown in Table 4. Sex attribution with the two analyses coincide in 19 of the 28 ungrouped cases (68.9%), and both discrimi-

nant analyses show significant intragroupal variability that needs to be taken into account for the interpopulation variability analysis.

Age-related variability. Overall age-related significant differences were found only for the standard deviation of all striations (ST, $F = 3.36$, $P = 0.0393$). However, combined effects of sex and age also showed significant differences for the length and standard deviation of the length of the distomesial and all striations (XT, ST, XDM, and SDM variables) (Table 3). Age-related differences in the buccal striation pattern have been observed in previous studies (Pérez-

TABLE 4. Prediction of sex for ungrouped teeth using the discriminant functions derived from the 15 striation variables analyzed¹

		Predicted group				Actual Group	Predicted sex	% Probability of sex				
		Highest		Second				Male		Female		
		Group	P (%)	Group	P (%)			First	Second	First	Second	
1	AT-10	3	99	7	1	3 or 7	Female	1	34	99	66	
2	AT-11	6	30	5	24	2 or 6	Male	82	73	18	27	
3	AT-12	1	54	7	24	3 or 7	Male	61	77	39	23	
4	AT-20 ²	4	100			3 or 7	?	0	78	100	22	
5	AT-22	15	4	40	5	25	1 or 5	?	49	85	51	15
6	AT-26		7	83	5	16	3 or 7	Female	17	27	83	73
7	AT-68		7	59	5	32	3 or 7	Female	39	62	61	38
8	AT-138 ²		5	88	4	11	3 or 7	Male	88	87	12	13
9	AT-149 ²		3	99	7	1	1 or 5	?	0	70	100	30
10	AT-169	24	2	54	5	42	1 or 5	Male	96	97	4	3
11	AT-271	15	7	60	5	23	1 or 5	?	36	81	64	19
12	AT-279	17	3	60	5	23	3 or 7	Female	23	23	77	77
13	AT-286	14	7	81	5	8	1 or 5	?	17	63	83	37
14	AT-559		4	45	2	31	3 or 7	Female	32	30	68	70
15	AT-561		4	44	2	34	3 or 7	?	40	95	60	5
16	AT-562		5	79	1	14	1 or 5	Male	93	91	7	9
17	AT-563 ²		3	59	7	40	1 or 5	Female	2	3	98	97
18	AT-588 ²		7	73	2	26	1 or 5	Female	27	39	73	61
19	AT-746 ²		5	73	4	20	3 or 7	Male	75	91	25	9
20	AT-806 ²		1	36	4	24	3 or 7	Male	62	68	38	32
21	AT-807 ²		4	100			1 or 5	?	0	75	100	25
22	AT-813		5	52	7	40	1 or 5	Male	52	67	48	33
23	AT-817		5	85	7	15	3 or 7	Male	85	70	15	30
24	AT-819		7	51	5	26	3 or 7	?	49	56	51	44
25	AT-822		7	77	3	16	3 or 7	Female	7	19	93	81
26	AT-823 ²	17	2	68	4	22	3 or 7	Male	69	98	31	2
27	AT-824		4	100			3 or 7	?	0	89	100	11
28	AT-829		5	96	7	3	3 or 7	Male	96	90	4	10

¹ Predicted highest and second groups for the first discriminant analysis are as follows: 1, male, mandible isolated; 2, male, maxilla, isolated; 3, female, mandible, isolated; 4, female, maxilla, isolated; 5, male, mandible, in situ; 6, male, maxilla, in situ; 7, female, mandible, in situ; 8, female, maxilla, in situ. *P*% values are the probabilities of the first and second highest predicted group membership. Discriminant groups of the second analysis are as follows: 1, male, mandible; 2, male, maxilla; 3, female, mandible; 4, female, maxilla.

² No coincidence of predicted sex between the two discriminant analyses made and the actual expected group. A sex prediction was made only if the two discriminant analyses were concordant in their predictions.

Pérez et al., 1994), and thus dietary analysis of buccal tooth striations have been generally applied only to adult individuals. The sample of individuals from Sima de los Huesos includes almost as many subadult (4–11 years old, $n = 3$; 12–17 years, $n = 11$) as adult (18–24 years, $n = 9$; 25–40 years, $n = 9$) individuals (Bermúdez de Castro and Nicolás, 1997). In the present study, only three age groups have been considered (12–17, 18–24, and 25–40 years old). If sexes are lumped together, a discriminant analysis of all three age groups yields a correct classification probability of 63.86%. Separate analyses for each sex show probabilities of 78.72% for males and 77.87% for females. Significant differences are found (one-way ANOVAs with Bonferroni pair-groups correction) between the 12–17- and 25–40-year-old groups for males ($F = 13.42$, $P = 0.0000$) and

between the 18–24- and both the 12–17- and 25–40-year-old groups for females ($F = 5.38$, $P = 0.0082$). Subadult teeth tend thus to differ from adult teeth in the striation pattern, but the two adult groups also differ in the female group. Figure 4 shows average values of striation number and length by age groups. Female teeth have less and shorter striations than male teeth for all age groups, and the subadults (12–17 years old) have fewer striations than the adult groups.

Discriminant analysis of individuals by age and sex. A new sample of teeth was selected from the normal-density teeth ($n = 111$) for interpopulation comparisons. In this sample, all individuals were represented by a single tooth, considering the preference for the selection as M1 over Pm4 over M2 over Pm3 over M3 and left over right side when-

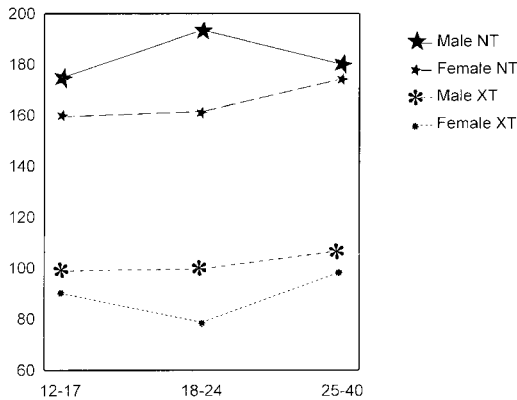


Fig. 4. Average values of total striation number and length (in micrometers) by age groups (12–17, 18–24, 25–40). Females tend to have less and shorter striations than males for all age groups (mandibles and maxillas together).

ever more than one tooth per individual was available. The attribution of teeth to identified individuals was taken from Bermúdez de Castro and Nicolás (1997). Teeth not ascribed to any individual or sex were not considered for interpopulation comparisons. One tooth per individual was analyzed within each one of the eight categories defined by the combined factors of age, sex, and maxilla. The groups obtained were as follows: 1) subadult, male, mandibular teeth ($n = 2$); 2) subadult, male, maxillary teeth ($n = 2$); 3) adult, male, mandibular teeth ($n = 5$); 4) adult, male, maxillary teeth ($n = 2$); 5) subadult, female, mandibular teeth ($n = 3$); 6) adult, female, mandibular teeth ($n = 6$); and 7) adult, female, maxillary teeth ($n = 2$). The sample sizes of each group are too low for analysis. However, the observed between-group variability is larger than the within-group, and thus subsampling by age, sex, and jaw is justified. The first two discriminant factors obtained explain 88.54% of the total variance, but only 40.9% of all cases are correctly classified. This is probably due to small sample sizes. If only the factors of age and sex are considered for the individual comparisons, four groups are obtained: 1) subadult males ($n = 2$); 2) adult males ($n = 5$); 3) subadult females ($n = 3$); and 4) adult females ($n = 6$) (a total of 16 individuals). A discriminant analysis of these groups yields three discrim-

inant functions explaining 96.91%, 2.49%, and 0.60% of the total variance, respectively, with a 100% correct classification probability. Figure 5 shows the 95% equiprobable ellipses of this analysis along with the individuals included in each group. The subadult male group includes individuals II and XX, the adult male group includes individuals VII, XII, XIII, XXII, and XXVII, the subadult female group includes individuals X, XI, and XXIII, and the adult female group includes individuals I, III, VI, and XIX. In Figure 5, the second axis discriminates subadult (negative values) from adult individuals (positive values), while the first axis shows close affinities between subadult males and adult females and between subadult females and adult males. The first function obtained is mainly correlated with the standard deviation of the length of the mesio-distal striations (SMD, $r = 0.28$), and the second is negatively correlated with the number of vertical striations (NV, $r = -0.21$) and positively with the number of horizontal striations (NH, $r = 0.16$).

Discriminant analysis of populations.

The classification of the sample from Sima de los Huesos with regard to the previously studied modern hunter-gatherer populations (Lalueza et al., 1996) shows clear differences among groups. Figure 6 shows the 70% equiprobable ellipses of all groups considered for the first two discriminant functions derived from the discriminant analysis of the four groups of modern populations indicated in Lalueza et al. (1996): vegetarian (V) Hindus ($n = 20$), carnivorous (C) hunter-gatherers ($n = 62$; includes aborigines from Tierra del Fuego, Inuit from Greenland, Laps, and Vancouver Indians); hunter-gatherers from arid (A) environments ($n = 44$; includes Bushmen, Australian aborigines, and Tasmanians), and hunter-gatherers from tropical (T) forests ($n = 27$; Vedddhas and Andaman Islanders). In the present study, a discriminant analysis equivalent to that in Lalueza et al. (1996), obtained with a stepwise method, was done (data comes from Lalueza, 1991). However, prior probabilities were now computed from sample sizes instead of equal probabilities for each group, and separate

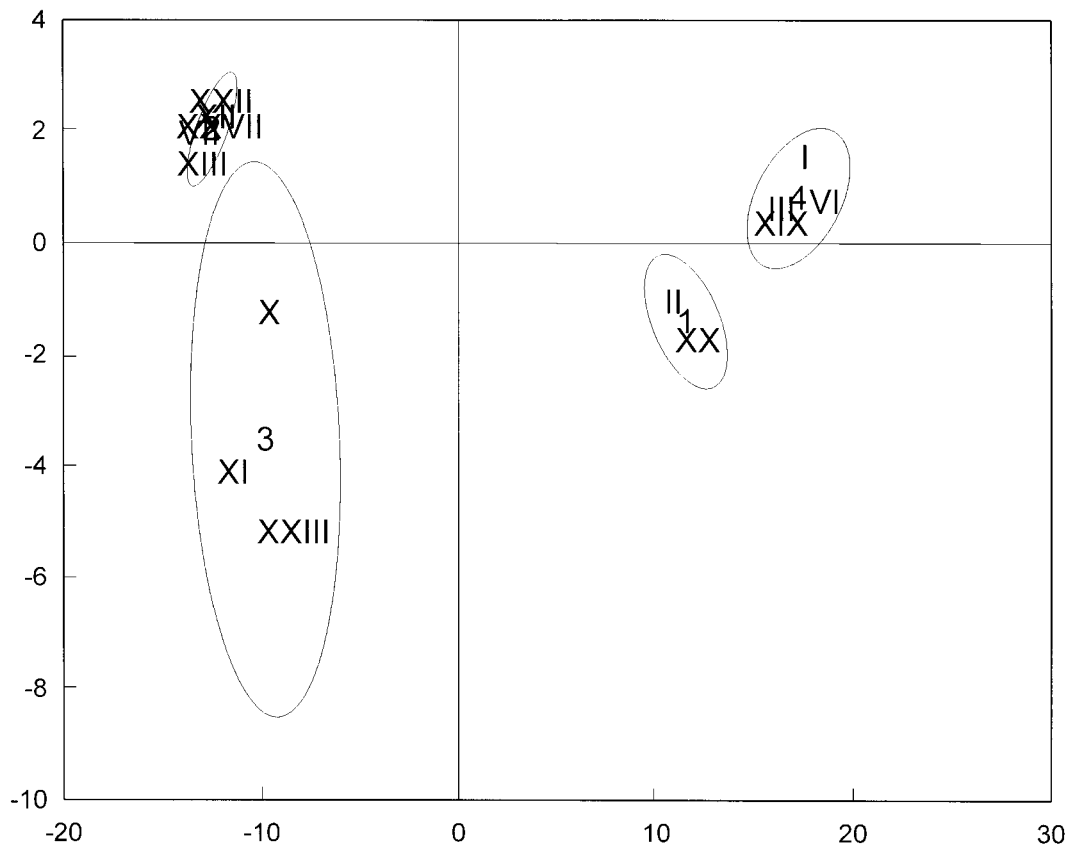


Fig. 5. Ninety-five percent equiprobable ellipses for the first two functions obtained with the discriminant analysis of teeth only for the factors of age and sex (not the maxilla factor), also considering one tooth per individual. Numbers located at the centroids of each ellipse are groups of subadult males (1) ($n = 2$), adult males (2)

($n = 5$), subadult females (3) ($n = 3$), and adult females (4) ($n = 6$), for a total of 16 individuals. Negative values for the y-axis include subadults. No overlapping of the ellipses is present. X-axis shows discriminant function 1; Y-axis, function 2.

covariance matrices were used to classify individuals instead of the combined covariance matrix. This procedure improves the classification when sample sizes vary among groups. The percent of correctly classified individuals obtained is 71.24%, and the first two factors explain 97.8% of the total variance (75.5% for the first function and 22.3% for the second). The first discriminant function is highly correlated with the number of horizontal striations (NH, $r = 0.92$) and negatively correlated with the length of the vertical ones (XV, $r = -0.34$). The second function is positively correlated with the total number of striations (NT, $r = 0.62$) and with the number of vertical (NV, $r = 0.59$) and mesio-distal (NMD, $r = 0.54$) striations

and negatively correlated with the average length of the horizontal (XH, $r = -0.27$) and all striations (XT, $r = -0.46$) and their standard deviations (SH, $r = -0.25$; ST, $r = -0.33$). Therefore, the first function mainly indicates number of horizontal striations, and the second combines number of striations and length. The discriminant factor coefficients for the teeth from Sima de los Huesos were computed using the discriminant functions derived from the discriminant analysis of the hunter-gatherer groups. The differences between the samples from Sima de los Huesos and the other groups (shown in Fig. 6) are mainly caused by shorter but more numerous striations in the Sima de los Huesos sample than in the

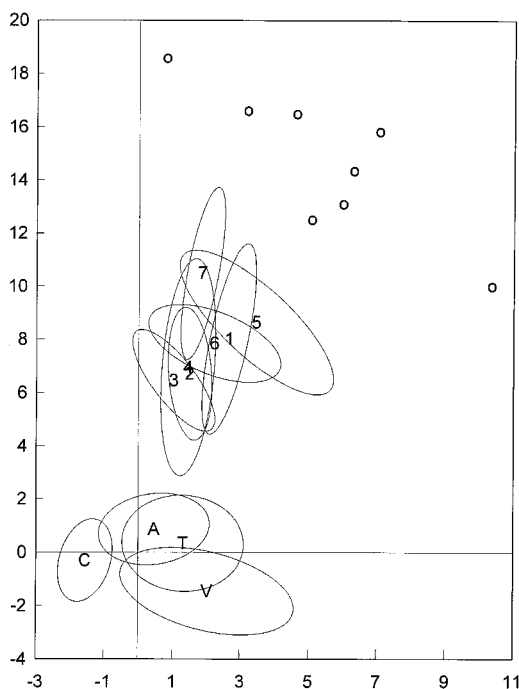


Fig. 6. Seventy percent equiprobable ellipses for the first two discriminant functions derived from the four groups of modern populations considered: vegetarian (V) Hindus ($n = 20$), carnivorous (C) hunter-gatherers ($n = 62$; includes aborigines from Tierra del Fuego, Inuit from Greenland, Laps, and Vancouver Indians), hunter-gatherers from arid (A) environments ($n = 44$; includes Bushmen, Australian Aborigines, and Tasmanians), and hunter-gatherers from tropical (T) forests ($n = 27$; Vedddhas and Andaman Islanders). The ellipses with numbers at the centroid are subsamples of teeth from Sima de los Huesos defined by the groups indicated in Fig. 3, and the open circles are high-density micrographs, all of which have been classified using the discriminant functions derived from the discriminant analysis of the hunter-gatherer groups.

hunter-gatherer groups (Lalueza et al., 1996). Figure 6 also shows the divergent position of the high-density teeth with regard to the hunter-gatherer groups.

Tooth size and striation pattern. Differences in tooth size at Sima de los Huesos have been explained in terms of sexual dimorphism of the mandible (Rosas, 1995; Bermúdez de Castro, 1986; 1988), and crown area has been used to sex some individuals (Bermúdez de Castro, 1993; Bermúdez de Castro et al., 1993; Bermúdez de Castro and Nicolás, 1997). The gradient in size and shape observed in the mandibles from Atapuerca might also be explained by growth

processes, perhaps sex-related, associated with taxonomically significant features (Rosas, 1997). However, attribution of isolated teeth to a specific sex group only by a size criterion may be somewhat problematic since, in the SH sample, large teeth are not consistently associated with large and more robust mandibles or skulls (Bermúdez de Castro and Nicolás, 1997). For instance, Skhul 5 and mandible AT-792 show robust morphological traits but have tooth sizes compatible with present-day populations (Rosas, 1997). Significant Spearman correlation coefficients are found here between sex and the bucco-lingual diameter (BLD) for Pm_4 ($r_s = 0.70$, $P = 0.006$, $n = 14$) and M_3 ($r_s = 0.87$, $P = 0.000$, $n = 11$) and for M_2 ($r_s = 0.80$, $P = 0.035$, $n = 7$). Since significant differences in the buccal striation pattern have been observed between sexes, a significant correlation between the striation pattern and tooth size should also be observed. Pearson correlation coefficients between the BLD and the striation pattern variables, by maxilla and tooth, show significant P values only for variables XMD ($r = 0.55$, $P = 0.042$, M_2 $n = 14$), XDM ($r = -0.61$, $P = 0.034$, M_3 $n = 12$), SMD ($r = 0.57$, $P = 0.035$, M_2 $n = 14$), and SDM ($r = -0.50$, $P = 0.048$, Pm_4 $n = 16$). As expected from the results in Table 3, the length of the striations rather than the number of striations is the variable that better discriminates between sexes. The total number of striations (NT) is significantly correlated with the bucco-lingual tooth diameter only if the whole sample is considered ($r = 0.23$, $n = 108$, $P = 0.016$), though with a low correlation value, but no significant correlations are found by groups of sex and maxilla.

DISCUSSION

High-density teeth

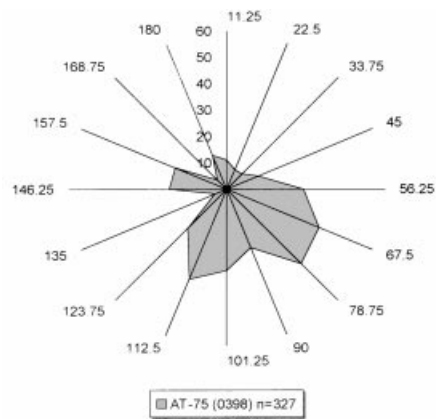
In previous studies, we showed that the number of striations is the main source of variation explaining interpopulation variability and that the striation pattern is highly dependent on ecological factors associated with food availability. However, in the Middle Pleistocene sample from Sima de los Huesos, the high striation densities observed in some of the teeth studied could be attributed to postdepositional processes affecting the teeth as well as to differential

dietary habits of the individuals affected. Postmortem wear may not be ruled out a priori given the 300,000 BP dating of the remains, and it may be responsible for the enamel damage observed in some teeth (high striation densities, enamel breakage, enamel prisms, and dentine exposure). The deposits in which the teeth were found consist of a fine breccia with a clayish matrix, without a high abrasive potential, formed without significant transportation in motionless bodies of water (Bischoff et al., 1997). The human SH fossils might be in situ remains, as argued from the spatial distribution of the bones and teeth (Arsuaga et al., 1997). Some isolated teeth of the same individual were found close to each other in the same deposits, which argues against dispersion and long postdepositional transportation processes. However, Andrews and Fernández (1997) have described some evidence of movement of bone. For these authors, carnivores might have preyed upon humans, and the residual human bones would have been transported into the SH cave system by mud flow, producing postdepositional breakage and rounding of the bones (Andrews and Fernández, 1997). Otherwise, postdepositional changes might have occurred (Teaford, 1988) as a result of sediment movement within the chamber.

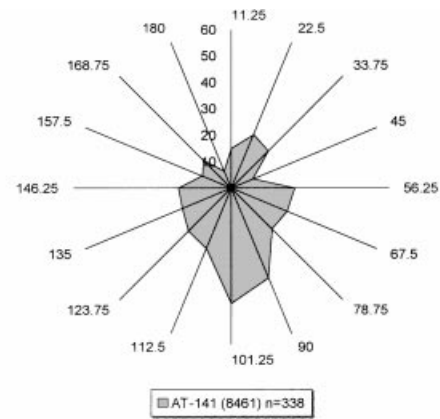
The high density of striations observed in some of the teeth studied strongly suggests that some type of postmortem wear may have altered the enamel surface. Not all teeth of identified individuals have high densities of striations, as would be expected if taphonomic processes had affected teeth and individuals in the same manner. The high-density effect is present both in isolated and in situ teeth with no differentiation by maxilla, tooth, or individual. Nine of the 20 individuals in the sample have only one affected tooth, and two individuals (VII and XV) have two teeth affected; four affected individuals are females, and also four are males; only two of the 13 affected teeth are maxillary teeth; two are Pm3, one is Pm4, six are M1, three are M2, and one is M3; five are left-sided and eight right-sided; six of the affected teeth were found in nondisturbed, in situ deposits, and seven were in disturbed sediments. Finally, not all ana-

lyzed areas of the same tooth showed the high-density pattern. The number of teeth with a high density of striations is rather small (13 from 124; 10.5%), and no consistent pattern, intraindividual or intrapopulational, is evident. If dietary differentiation of individuals were responsible for the differences between normal and high-density teeth, a consistent interindividual differentiation pattern would be expected. A stochastic postdepositional process affecting teeth rather than individuals seems a more likely cause for the high-density effect. Handling alterations and cleaning of teeth can be ruled out because all affected teeth correspond to the more recent materials that were carefully cleaned and stored. Other causes may relate to special postmortem use of certain teeth before deposition.

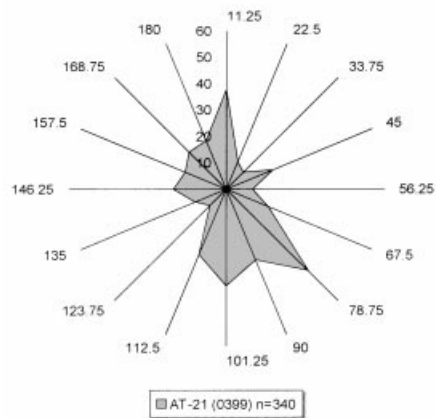
Postmortem wear has been previously described to affect Primate occlusal tooth surfaces (Teaford, 1988). However, no comparable alterations have ever been found by us on the buccal surface of human teeth, where no significant pitting occurs, not even on the teeth from Arago (400,000 BP) and Hortus (Würm II) that we are analyzing at present or in the Neanderthal remains previously studied (Lalueza et al., 1996). If postmortem wear were the only source of striations on the buccal surface of teeth, a random pattern of orientations would be expected, since no preferential direction of abrasive particles in the sediments is likely. Figure 7 shows the absolute frequencies of striations by orientations (11.25° ranges) of all the high-density affected teeth along with two nonaffected (AT-26, AT-279) micrographs and the average frequencies of orientation for the affected group ($n = 15$) and the nonaffected sample ($n = 128$). The affected sample shows a high average frequency of striations for all orientations, but the vertical direction (67.5–112.5°) seems to be specially affected in all cases except in Figure 7l,m, both with many 112.5–135° striations, and Figure 7n, with many 45–67.5° striations. No distinct pattern of predominant increase in frequency of striation in the affected teeth by side (left, right) is present. While some right teeth have more disto-mesial striations, others have more mesio-distal ones; and the same is true for the left teeth. What is clear



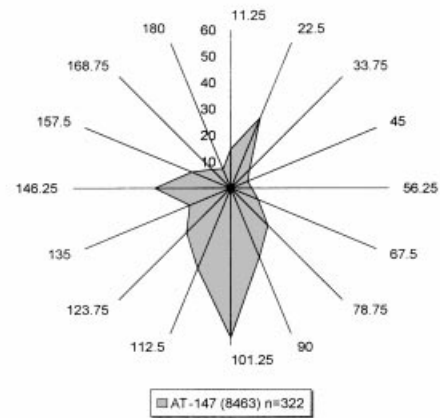
a) Ind. 6, M2 Mandible Left. Female



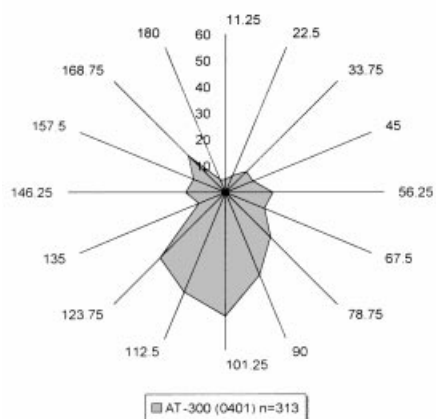
b) Ind. 10, M1 Mandible Right. Female



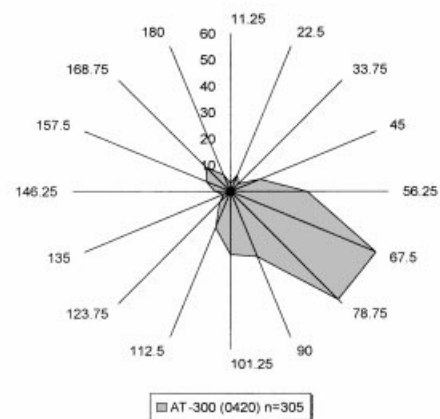
c) Ind. 7, M1 Mandible Left. Male



d) Ind. 7, Pm4 Mandible Left. Male

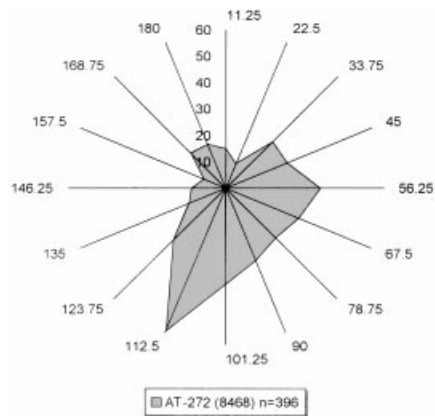


e) Ind. 12, M1 Mandible Right. Male (mesial)

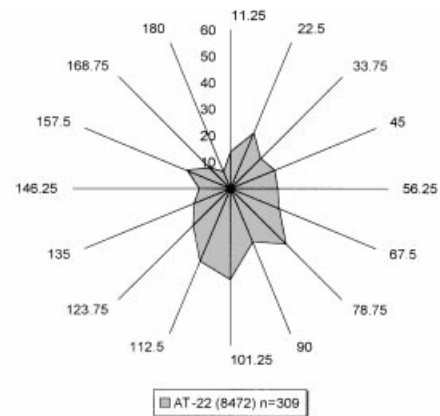


f) Ind. 12, M1 Mandible Right. Male (distal)

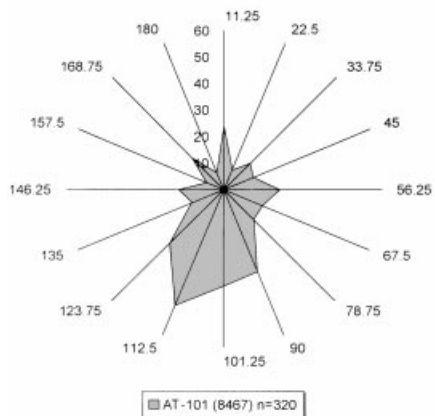
Fig. 7. (See legend page 454.)



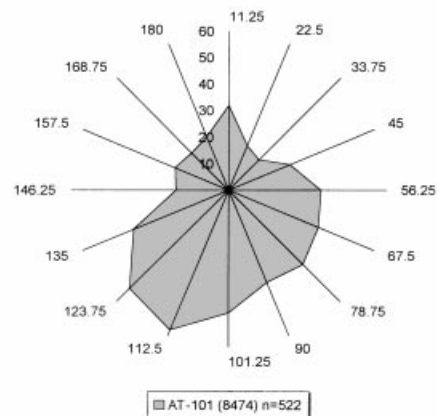
g) Ind. 14, M1 Mandible Right.



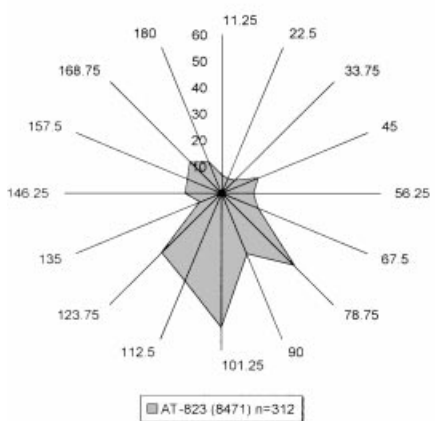
h) Ind. 15, M1 Mandible Left.



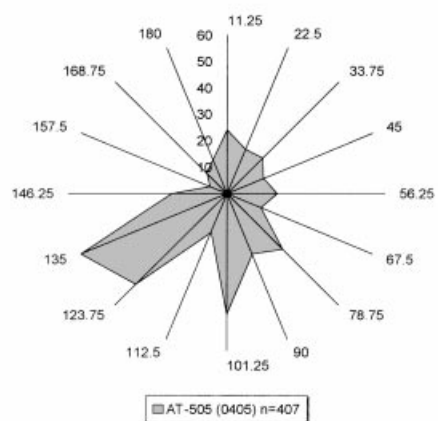
i) Ind. 15, M1 Mandible Right.



j) Ind. 15, M1 Mandible Right. (Lingual)

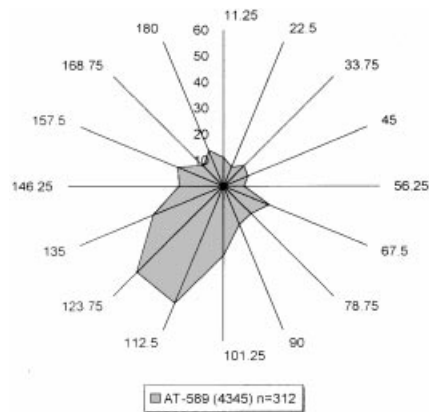


k) Ind. 17, Pm3 Manxila Right.

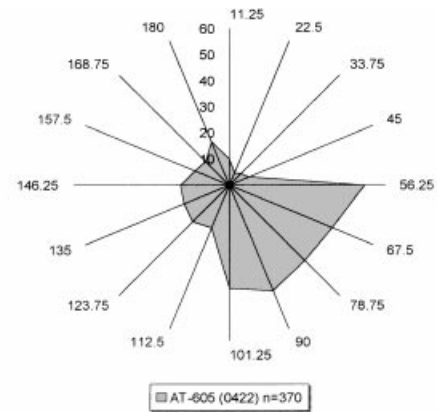


l) Ind. 19, M2 Mandible Leftt. Female

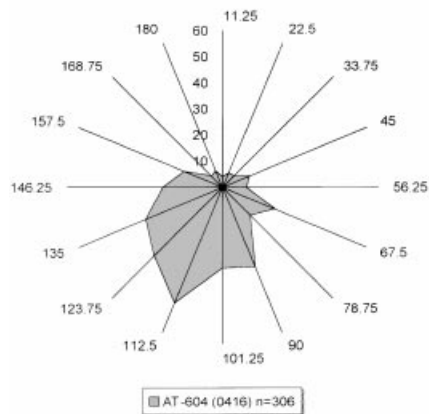
Fig. 7. (See legend page 454.)



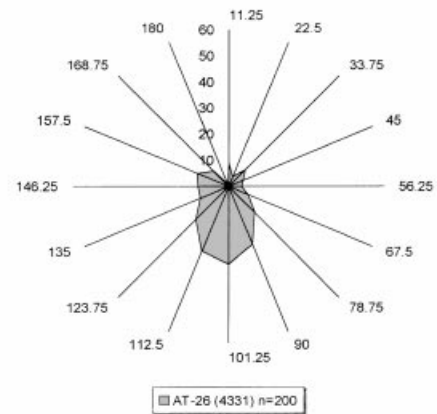
m) Ind. 20, Pm3 Manxila Right. Male



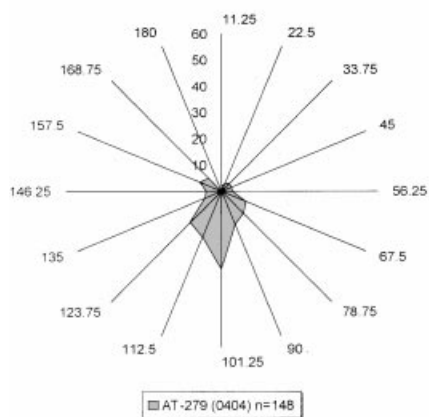
n) Ind. 22, M2 Mandible Right. Male



o) Ind. 25, M3 Mandible Right. Female



p) Ind. ?, M1 Manxila Right



q) Ind. 17, Pm4 Manxila Right. Male

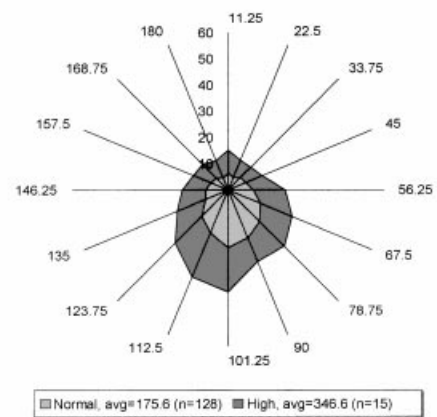
r) Average values for *Normal* and *High* densities

Fig. 7. Frequency distribution of striation orientations (from 0–180°) by 11.25° ranges, both for the 15 high-density micrographs—AT-75 (a), AT-141 (b), AT-21 (c), AT-147 (d), AT-300 (e) mesial, AT-300 (f) distal, AT-272 (g), AT-22 (h), AT-101 (i), AT-101 (j) lingual, AT-823 (k), AT-505 (l), AT-589 (m), AT-605 (n), and AT-604 (o)—, two of the normal-density ones—AT-26 (p), and AT-279 (q)—and average values both for the normal (interior area) and the high-density (darker exterior area) groups (r).

from Figure 7, though, is that the striations with a vertical or close to vertical direction are always more abundant than the horizontal or close to horizontal ones, both in the normal and the high-density groups. If postmortem wear were responsible for the increase of striation frequencies observed, a more stochastic pattern would be expected (i.e., more horizontal striations would be present). Postmortem unidirectional wear, such as the dragging of teeth with sediment movement, could account for the pattern of striation orientation observed in the high-density micrographs, but all orientations would be expected to be equally likely. If sediment movement and trampling in the site is not yet discarded for Sima de los Huesos (Andrews and Fernández, 1997), a certain degree of postmortem wear could account for the striation densities observed. Although postdepositional abrasives might have affected all teeth and tooth surfaces in similar ways, a certain degree of variability might be expected. In fact, the factor of position (isolated or in situ teeth) was shown to be responsible for some of the striation pattern variability observed. Isolated teeth tend to have less but longer striations than in situ teeth, which have more and shorter striations for all orientations. Thus, in situ teeth might have been more affected by postmortem wear, perhaps because they offer higher resistance to sediment movement than isolated teeth. Also, direct carnivore activity upon human bones and teeth, as suggested by Andrews and Fernández (1997), might be responsible for at least some of the striations observed on the teeth.

Larger samples and further comparisons with other ancient hunter-gatherer populations are needed to test hypotheses about postdepositional tooth wear. Specially, the analysis of the interproximal wear facets (Teaford, 1988) will allow the characterization of postmortem damage in the SH sample. Nevertheless, the intrapopulation variability observed, with age-, sex-, and maxilla-related differences in the striation pattern, strongly supports the hypothesis that postmortem wear has not affected all teeth in a generalized manner since biological correlates are found that explain the striation variability observed: mechanical differences

in the chewing of food between the mandible and the maxilla, sex-related dietary and food behavior differences, and age-related differences in diet. From the analyses done, we suggest that at the SH site postmortem wear has affected only some teeth, and more precisely only some enamel patches of some teeth in a much higher degree than others. This would account for the stochastic presence of high-density areas within individuals and teeth, and it is consistent with a nonuniform and noncontinuous model of carnivore dispersion of bones and teeth associated with some type of mild process of sediment movement that would not affect all teeth in the same manner.

Intrapopulation variability

No direct dietary implication can yet be drawn from this analysis of the normal density sample, except that the Middle Pleistocene population from Sima de los Huesos might have had more abrasive dietary habits that produced more striations and a higher variability of the striation pattern than modern hunter-gatherer populations. However, it is difficult to imagine that the Kalahari San or Australian aborigines would have had a less abrasive diet than the Atapuerca hominids. Significant differences in tool technologies and food-processing techniques might account for the differences observed. The sex-related differences observed suggest that females are probably eating more variable or even different food resources than males since they have significantly longer striations than males and can be clearly discriminated from the striation pattern. Sex-related differences in diet and dietary behavior among hunter-gatherer populations have been ethnologically documented for numerous modern aboriginal groups around the world, though no direct evidence has ever been observed in fossil populations other than that derived from behavioral inference. If the striation pattern depends on ecological and dietary variables, the sexual dimorphism observed would be informative of distinct ecological strategies of males and females in the Middle Pleistocene population of Atapuerca. Age-related differences in the buccal striation pattern have also been observed in previous studies

(Pérez-Pérez et al., 1994). In the SH sample, a certain increase in the number of striations with age can be observed (Fig. 4), suggesting that subadults might have a slightly less abrasive diet than adults. However, a high degree of overlapping of the confidence intervals occurs, suggesting that the young individuals studied (between 12 and 17 year of age) might have had a diet with a similar abrasive potential to that of the adult individuals. The differences observed in the striation pattern between mandibular and maxillary teeth show that in both sexes the maxillary teeth have more striations than the mandibular ones, but females show longer striations in the mandibular teeth. Mechanical forces during the process of chewing might account for the higher number of striations in maxillary teeth, and differences in the consistency of the foods eaten by females could explain the longer striations in mandibular teeth of the female group.

CONCLUSIONS

As a whole, the analyses done in the sample of teeth from the SH site suggest that high degrees of intrapopulation variability of the buccal striation pattern should be expected when studying human fossil populations. The analysis of isolated specimens might not be clearly informative of dietary habits of fossil remains. The significant intragroup differences observed may be caused by behavioral and dietary differences among sex and age groups, indicating that the analysis of the buccal striation pattern can be of great relevance for dietary analysis of fossil populations. Although large samples of biologically distinct fossil populations are rarely available, an extensive study of the population variability of the buccal striation pattern, both of Primates and hominids, needs to be done. Modern hunter-gatherers' buccal striation pattern seems not to be a good dietary reference for fossil populations since they seem to have much less abrasive diets. A new paradigm needs to be built with well-represented fossil populations where intrapopulation variability could be analyzed and compared with other human groups. Also, postdepositional damage on the buccal surface of fossil teeth needs fur-

ther analysis, including analysis of nonexposed enamel surfaces, such as in unerupted teeth or in the interstitial facets. Finally, the Sima de los Huesos materials need exhaustive study with larger subgroup sample sizes. However, the approach followed here gives important clues about the relevance of the study of the buccal microwear for the inference of feeding adaptations in fossil humans, as has already been suggested for fossil primates (Ungar and Teaford, 1996).

ACKNOWLEDGMENTS

Funding for this research was provided in part by Spanish MEC grants DGICYT PB-93-0066 and PB-93-0021 and PB-96-1026. SEM micrographs were obtained at the Serveis Científicotécnicos de la Universitat de Barcelona. P. Ungar, M. Teaford, and anonymous referees greatly contributed to the final version of this paper. English editing was done by Jessica J. Lockhart (STI, Servicios de Traducción e Interpretación).

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